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Vol. 49 No. 1

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1922

Epiphyllous plants of certain regions in Jamaica*

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(WITH PLATE I AND ONE TEXT FIGURE)

The great variety and luxuriant growth of the epiphyllous plants seen in Jamaica in the summer of 1919 led the writer to study them from two points of view: first, their distribution in relation to climatic conditions; second, their histological relation to the leaves bearing them, in order to determine whether these epiphytes are to any degree parasitic. The study of the distribution and environment of the epiphyllous plants was made in the field. The relation of the epiphyll to its supporting leaf was studied by histological methods in the laboratory.

HISTORICAL

Very little is known about epiphyllous plants today, in spite of the fact that they have long interested botanists. As early as 1875 Berkeley (1) reported the occurrence of epiphyllous lichens growing on the leaves of the tea plant; some of these apparently epiphyllous forms showed marked parasitic adaptation. Such forms were found in abundance in warm moist regions. Two of the forms observed by Berkeley were regarded as species belonging to the genus *Strigula*.

A few years after Berkeley's paper appeared, Cunningham (2) reported on an epiphyllous lichen and an epiphyllous alga, *Mycoidea parasitica*, parasitic on leaves of *Mangifera indica*, *Croton* and *Rhododendron*.

[The BULLETIN for December (48 : 315–363) was issued February 28, 1922.]

* Botanical Contribution No. 69 from the Johns Hopkins University.

Marshall Ward (6) worked on an epiphyllous lichen which he believed to be the one worked on by Cunningham. He observed no penetration of the tissues of the supporting leaf by the lichen and therefore decided that it was not parasitic. He did find, however, one or more cross walls in the palisade cells of the supporting leaf beneath the epiphylls, which formed three or four layers of these cells instead of the normally single layer.

Schmidle (5) found species of *Trentepohlia arboreum* and *T. aurea* as well as *Phycopeltis microcystis* quite common as epiphyllous forms in Samoa. Massart (3) found that some orchids pass their entire existence on a single leaf. He found also that the epiphyllous floras differ in different regions. Algae and liverworts are the most common epiphyllous forms, while mosses acquire the epiphyllous habit only in very humid ravines.

OBSERVATIONS AND METHODS

Specimens of epiphyllous plants were collected in various regions in the Blue Mountains of Jamaica. The field observations were made during June and July, 1919, in the following places: Cinchona Plantation (5,000 feet), Morce's Gap (4,934 feet), New Haven Gap (5,600 feet), Green River Valley (3,000 feet), Markham Hill (5,800 feet), Vinegar Hill Road (4,500 feet), Clyde River Valley (4,500 feet) and Blue Mountain Peak (7,428 feet).

Material was either pressed or preserved in glycerine in 4 per cent formaldehyde, or in 60 per cent alcohol. For careful histological study, material was fixed in chromoacetic acid and preserved in 70 per cent alcohol until finally dehydrated, embedded, cut and stained with the Flemming's triple stain. In some cases material was left unstained for comparison.

The Cinchona Plantation is situated on a spur running south from the Blue Mountains at five thousand feet above sea level. The temperature varies between the extremes of 48° and 82° F. The vegetation of the garden about the residence of the Cinchona Plantation consists largely of introduced plants, many of which are Himalayan, Australian and Cape of Good Hope species. There are also native tree ferns, orchids, bromeliads, and many other transplanted native species. The banks along the trails outside the garden are covered mostly by native ferns interspersed with, or on the north side of Cinchona Hill largely replaced by, *Hedychium coronarium.*

During the wet season Cinchona is enveloped in clouds for days at a stretch and the rains are very heavy and frequent. In spite of this abundance of moisture at certain times of the year, epiphyllous plants are rather scarce on the south side of Cinchona Hill. Only one hepatic, two species of algae and a few kinds of lichens were found growing there. Of these *Trentepohlia* grows in damp or shaded places on the ground, on the bark of trees and on the leaves of certain plants. Lichens, the most common of which belong to the genus *Sticta,* grow abundantly on certain plants. Some of the leaves of *Callistemon lanceolatum,* for instance, are almost completely covered by this lichen. In a few cases the leaves of *Hedychium* were found sprinkled with a reddish disk-like alga belonging to the genus *Phycopeltis.* The epiphyllous flora of this region is evidently not a rich one (see TABLE I, A).

At Morce's Gap, two miles north of Cinchona and at about the same level, is found a characteristic tropical montane rain forest. Here moisture is abundant at all seasons of the year. On the windward side of the mountains everything reeks with moisture; clouds drift constantly through these dense forests and rain falls frequently during eight months of the year. The dense vegetation, except on the ridges, is usually dripping wet. Very rarely do the sun's rays penetrate to the floor of these forests. Ferns carpet the floor and cover the walls of the steep-sided ravines. Tree ferns, such as *Alsophila* and *Cyathea,* are very common, many of them having trunks four or five inches thick and thirty feet high or more. Species of the genera *Marattia, Danaea, Polypodium* and *Elaphoglossum* are very abundant. Such forms as *Blechnum attenuatum* and many species of *Trichomanes, Hymenophyllum, Polypodium* and *Elaphoglossum* have been compelled to adopt either the climbing or the epiphytic habit in the intense competition for sunlight. *Podocarpus, Hedyosmum,* species of *Piper* and many other dicotyledonous trees and shrubs, together with numerous herbaceous plants, are scattered through these woods, increasing the struggle for existence and making the competition for light more keen.

In such an environment epiphyllous plants are very abundant.

TABLE I

Epiphyllous plants of Jamaica

Region	Supporting plant	Algae	Lichens	Hepaticae	Musci
A. Cinchona Plantation, 5000 ft. alt.; South exposure.	*Callistemon lanceolatum*		*Parmelia* sp. *Sticta* sp. *Usnea* sp. A form of Pilocarpaceae	*Cololejeunea diaphana*	
	Hedychium coronarium	*Phycopeltis* sp. *Trentepohlia aurea*	*Lopadium* sp.		
	Pittosporum tobira	*Phycopeltis* sp.			
B. Morce's Gap, 4934 ft. alt.; north exposure.	*Elaphoglossum latifolium*	*Desmidium* sp. *Nostoc* sp. *Phycopeltis* sp. *Pinnularia* sp. *Scytonema* sp. *Staurastrum* sp.		*Cololejeunea* sp. *Cololejeunea diaphana* *Crossotolejeunea* sp. *Diplasiolejeunea pellucida* *Metzgeria furcata* *Microlejeunea* sp. (?)	
	Hedychium coronarium	*Phycopeltis* sp.		*Crossotolejeunea* sp. *Aphanolejeunea* sp. *Metzgeria furcata* *Cololejeunea diaphana* *Diplasiolejeunea pellucida* Schiffn.	
	Hedyosmum arborescens Sw.			*Crossotolejeunea* sp. *Lejeunea flava*	

TABLE I—*Continued*

Region	Supporting plant	Algae	Lichens	Hepaticae	Musci
B. Morce's Gap—*Continued.*	*Mangifera indica*	*Phycopeltis* sp.	Undetermined species*		
	Podocarpus coriaceus	*Phycopeltis* sp.		*Crossotolejeunea* sp. *Lejeunea flava*	
	Polypodium sp.		Undetermined species*		*Clastobryum americanum*
C. New Haven Gap, 5600 ft. alt.; north exposure.	*Stelis ophioglossoides*	*Phycopeltis* sp. *Trentepohlia aurea*			
	Trichomanes sp.			*Crossotolejeunea* sp.	
	Blechnum attenuatum	*Phycopeltis* sp. *Pinnularia* sp. *Nostoc* sp. *Scytonema* sp.		*Cololejeunea diaphana* *Crossotolejeunea* sp. *Diplasiolejeunea pellucida* *Drepanolejeunea campanulata* *Lophocolea* sp. *Metzgeria furcata* *Taxilejeunea* sp.	*Mittenothamnium reptans*
	Clusia havetioides	*Pinnularia* sp. *Nostoc* sp. *Scytonema* sp.	*Parmelia* sp.	*Aphanolejeunea* sp. *Aphanolejeunea sicaefolia* *Diplasiolejeunea pellucida* *Drepanolejeunea campanulata* *Cololejeunea diaphana* *Lejeunea flava* *Metzgeria furcata* *Microlejeunea* sp.	*Mittenothamnium reptans*

* Up to the present the writer has been unable to have some of the epiphyllous lichens definitely determined.

TABLE I—*Continued*

Region	Supporting plant	Algae	Lichens	Hepaticae	Musci
New Haven Gap—*Continued.*	*Monoclea Gottschei*				*Mittenothamnium reptans*
	Plagiochila sp.			*Riccardia* sp.	*Mittenothamnium reptans*
	Rhododendron sp.		*Phylloporina epiphylla* Undetermined species		
D. Vinegar Hill Road, 4500 ft. alt.: north and west exposures.	*Asplenium* sp.			*Cololejeunea* sp. *Cololejeunea diaphana* *Crossotolejeunea* sp. *Diplasiolejeunea pellucida* *Drepanolejeunea campanulata* *Metzgeria furcata*	
	Clusia havetioides	*Nostoc* sp. *Phycopeltis* sp. *Pinnularia* sp.	*Parmelia*	*Cololejeunea* sp. *Diplasiolejeunea pellucida* *Drepanolejeunea campanulata* *Lejeunea flava* *Lophocolea* sp. *Metzgeria furcata* *Taxilejeunea* sp.	
	*Elaphoglossum latifolium**	*Chroococcus* sp. *Gleocapsa* sp. *Nostoc* sp. *Phycopeltis* sp. *Scytonema* sp.		*Cololejeunea diaphana* *Crossotolejeunea* sp. *Lejeunea flava* *Metzgeria furcata*	*Mittenothamnium reptans*

* On a leaf of this species the seed plant *Caraguta Sintenesii* was likewise found living as an epiphyll.

TABLE I—*Continued.*

Region	Supporting plant	Algae	Lichens	Hepaticae	Musci
D. Vinegar Hill Road—*Continued.*	*Epidendrum* sp.		Undetermined species.	*Drepanolejeunea campanulata*	
	Polypodium Phyllitidis			*Cololejeunea* sp. *Cololejeunea diaphana* *Crossotolejeunea* sp. *Diplasiolejeunea pellucida* *Drepanolejeunea campanulata* *Drepanolejeunea crucianella* *Lophocolea* sp. *Metzgeria furcata* *Taxilejeunea* sp.	*Fissidens* sp.
E. Blue Mountain Peak, 7428 ft. alt.; northeast exposure.	*Podocarpus coriaceus*	*Phycopeltis* sp.			
F. Clyde River Valley, 4000 ft. alt.; north and west exposures.	*Citrus Limonium*	*Phycopeltis* sp. *Scytonema* sp. *Trentepohlia aurea*	*Coenogonium* sp. *Collema* sp. *Lecanora* sp. *Pannaria rubiginosa* *Pyrenula* sp. Undetermined species.	*Aphanolejeunea* sp. *Cololejeunea* sp. *Diplasiolejeunea pellucida* *Drepanolejeunea campanulata* *Lejeunea flava* *Metzgeria furcata*	

Here one finds plants of many types growing on the soil; on these grow various plants as epiphytes and on these in turn grow other epiphytes. A remarkable diversity of epiphytic forms can be found on one plant, and some of the forms are wonderfully adapted to their epiphytic mode of life. These epiphytes occur on every patch of dead or living plant surface that receives even a moderate supply of light. One finds on a single leaf here such forms as algae, lichens, hepatics, mosses and, at times, even seed plants, not to mention occasional fungi and minute epiphyllous animals. It is rather strange that not a single fern prothallus has been found on any of the leaves of this region, though numerous sporangia were present and probably spores also on many different kinds of leaves. In TABLE I, B, are listed the different kinds of epiphyllous forms found near Morce's Gap.

The climatic conditions of New Haven Gap do not differ markedly from those of Morce's Gap. The temperature is nearly the same, ranging annually from 40.5° to 83° F., and the floor of the forest is constantly moist and shaded. Here again one finds the characteristic rain forest vegetation. The epiphyllous plants here are quite as abundant as at Morce's Gap and consist mainly of algae, hepatics, and mosses. The leaves of the climbing plants of this locality are well inhabited by epiphyllous forms. The leaves of *Clusia havetioides* and of such ferns as *Blechnum attenuatum*, *Elaphoglossum latifolium* and *Polypodium Phyllitidis* serve most frequently as the substratum for epiphylls (see PLATE 1). A glance at TABLE I, C, gives one a fair notion of the groups of epiphyllous plants found in the New Haven Gap region.

Going northward from Morce's Gap along the upper eastern slopes of the Mabess Valley the trail is particularly interesting as it presents a splendid view of the ravines. The crowns of the tree ferns carpet many side ravines of the valley. The huge lianes, the numerous orchids, the wild pines and the purplish filmy ferns mantle the branches of many trees and the species of *Asplenium*, *Blechnum* and *Polypodium*, along with the walking fern (*Polystichum plaschnichianum*), spread over the banks. One does not have to walk off the trail to find numerous epiphyllous plants. The upper leaves of many of the low trees on the Vinegar Hill Road are completely covered by them. TABLE I, D, shows the great variety of epiphyllous forms found in this region.

On TABLE I, E and F, are indicated the epiphyllous plants observed on the Blue Mountain Peak and in the Clyde River Valley. In the former, though there is always an abundance of moisture, the epiphyllous flora is not a rich one, owing probably to the frequent heavy rains, the rather low temperature and the occasional strong winds. Those of the Clyde River Valley occur chiefly on trees growing along streams, where there is sufficient shade and a humid atmosphere.

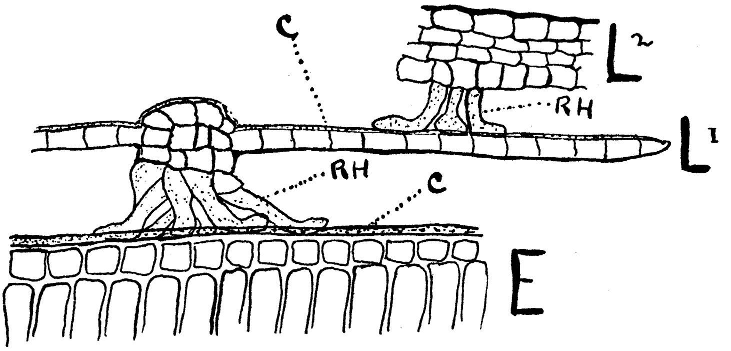

FIG. 1. Part of transverse section of a leaf of *Elaphoglossum latifolium* (*E*) with the rhizoids (*Rh*) of an epiphyllous liverwort (L^1) pressed into its cuticle. This liverwort in turn bears another epiphyllous liverwort (L^2), which is likewise attached by its rhizoids (*Rh*).

In general, observations in these Blue Mountains of Jamaica show that the epiphyllous members of each group of plants are limited to certain regions where climatic conditions are suitable for such growth. Thus, Algae, Hepaticae, and Musci usually thrive best on the windward side of the mountains and are abundant only in very damp and very shady woods. Epiphyllous lichens, on the other hand, do not require very warm, humid, and shady places but are also found in relatively dry regions. It was rather difficult to ascertain with any degree of definiteness the exact age of the leaves which bore epiphyllous plants, but it is safe to state that none are present on very young leaves. As a rule they do not appear on leaves until the latter are one or two seasons old.

In order to determine the relation between the epiphyllous forms and the plants on which they grow, cross sections were made of the leaves of *Elaphoglossum latifolium*, *Clusia havetioides*, *Polypodium Phyllitidis* and *Mangifera indica*. The leaves of *Elaphoglossum latifolium* were those chiefly used because of the abundance on them of epiphyllous liverworts in various stages of development. Sections of leaves of *Mangifera indica* were also studied to determine the relation of an epiphyllous lichen to the mango leaf.

Sections of the leaves bearing epiphyllous hepatics showed characteristic thickened, club-like rhizoids arising in groups from the stem of the creeping liverwort. These rhizoids are sunken into the cuticle of the supporting leaf as if pressed in by some external force. The rhizoids broaden at their lower ends and flatten out as is shown in TEXT-FIG. 1. This is true even of the rhizoids of one epiphyllous liverwort when growing upon another, for one sometimes finds two or more tiers of epiphylls growing upon a fern or a dicotyledon. The rhizoids of the upper hepatic are in such cases decidedly flattened against the delicate leaves of the lower liverworts. This too is shown in the figure. The important point to be noted is that the rhizoids of the epiphyllous form were not observed to penetrate the tissues of the supporting leaf. Nor was there evident any abnormality in the internal structure of the supporting leaf, such as might conceivably be produced by the shade or by the weight of the epiphylls on the leaf or, possibly, by some substance such as an organic acid excreted by the rhizoids on the liverwort.

The leaves of *Mangifera indica* bore numbers of orange-red disk-like plants of a species of *Phycopeltis*. Among these orange-red specks there were also minute grey patch-like lichens resembling those described by Cunningham (3) and Ward (9). The relation between these lichens and the mango leaf on which they grew has not been definitely determined. The sections of the mango leaf thus far studied showed no modifications of its tissues and no penetration by the lichens.

DISCUSSION

The problem of the evolutionary origin and individual development of the epiphyllous plants is a complex one which still requires much careful investigation. Schimper (4) observed that epiphytic seed plants commonly originate on their support through seeds.

The scattered seeds germinate on the trunk, branches, or leaves of a tree or shrub and, with adequate moisture and other nutritive material, develop into epiphytes. He divides the fruits and seeds of epiphytes into three categories: first, those transported by birds, monkeys and other tree-inhabiting animals; second, those which are very light and may be transported by the wind and which may readily catch in the crevices of the bark and germinate there; third, those seeds which are especially adapted to be carried by the wind. Such seeds usually possess either hairs or wings or inflated coats which aid their distribution.

It is conceivable that a great many of the epiphyllous forms here being considered arise from spores, for spores have been found on many leaves. The epiphyllous liverworts evidently arise often from gemmae, for many such gemmae in the process of development have been found on leaves. The spores of liverworts, on the contrary, have rarely been found germinating on leaves. The observations thus far made indicate that many an epiphyllous hepatic or moss makes its start on the host by creeping up the stem of the support from the ground or up the petiole from the stem. As it climbs upward it dies off from below and when its younger part reaches the leaves it spreads over the surface and becomes strictly an epiphyllous form. Secondly, epiphyllous forms may be lodged upon the host by the agency of water. When during a rain the water flows down over the leaves and branches of a tree in the rain forest, it breaks off the hepatics and mosses and other plants from the surface of the stem or leaf and washes them down on the leaves below, where they continue to grow, covering the leaf in the course of time with a dense mat. Such is probably the explanation of the fact that in most cases the lower leaves possess the greatest number of epiphyllous plants, though, of course, lower leaves are older, better shaded, and are surrounded by moist air. It is probable also that the epiphyllous plants found on the dorsal sides of certain overturned leaves arise in the manner just described. The fact that no epiphyllous plants were observed on the lower sides of leaves still in normal position is evidence that these plants are propagated largely by these fragments. If it were commonly by spores we should expect these, at least occasionally, to stick to the underside of a leaf. Such cases, however, are extremely rare. In a third possible method of dispersal, spores, gemmae, or seeds may be washed down by the dripping water from above, or may be blown from adjacent plants by the wind. This method is particularly common among algae and lichens. The first two types of vegetative propagation seem to be the commoner ones, for in many instances the epiphyllous forms growing on the stem have actually been observed to spread over the surface of the leaf. Moreover, many of the forms found on the leaves occur likewise on the stem of the supporting plant. This is particularly true of hepatics and mosses. In lichens, however, the case may be different. There the alga, as well as the component fungus, may often be present separately on the leaf; each may reach the leaf in the form of loose spores or fragments, and there combine to give rise to the lichen itself.

Massart (3) failed to find in Java any epiphyllous pteridophytes and phanerogams. In the tabulated lists of epiphyllous plants of Jamaica in this paper it will be noted that no pteridophytes have been found. Although many fern sporangia were observed among the epiphylls by the writer, no germinating fern spores or fern prothallia were seen. The writer, however, found a few epiphyllous phanerogams. These were very young plants of the genus *Caraguata* attached to the surface of the leaf, and apparently doing well. How much further their development would continue is hard to tell, for the substratum is not firm enough to support a mature wild pine; before the epiphyllous wild pine could have time to mature, the supporting leaf would probably be shed. The fact is, at all events, that no mature wild pines were found growing on leaves. According to Massart, the epiphyllous plants do not constitute a similar flora everywhere; in some localities this consists solely of thallophytes, in others of bryophytes. This is also true for Jamaica, where in certain regions only one type occurs, while in other regions numerous diverse forms are present.

Massart's suggestion that the leaf-inhabiting fungus has been derived from the epiphyllous plant is at least favored by the relation to its host of the alga *Cephaleuros*, which may have either the parasitic or the epiphytic mode of life. On the other hand, there are still some fungi which possess the epiphyllous habit, such as *Metiola astrina* and a few others. There seems little doubt that a careful study of epiphyllous plants would throw some light on the origin of parasitism, such as that of leaf-infesting fungi.

SUMMARY

1. Epiphyllous plants of diverse selected regions in Jamaica were studied in the field and collected for laboratory study in Baltimore.

2. The results of the field observations were tabulated so as to give at a glance a general idea of the distribution of these epiphyllous plants in relation to the altitude, average temperature, and average humidity of their various habitats.

3. The possible modes of attaining the epiphyllous position are:

(*a*) Continual growing forward and dying off below, of hepatics and mosses, until they reach and cover the leaf.

(*b*) By distribution of spores, gemmae or seeds through the agency of rain and wind. This is especially true for algae and fungi.

(*c*) Propagation by displaced fragments of mature lichens, hepatics, and mosses.

4. An abundance of humidity, moderate temperature, and a relatively calm atmosphere encourage an abundant epiphyllous growth.

5. Histological studies of epiphyll-bearing leaves of *Elaphoglossum latifolium*, *Clusia havetioides* and *Mangifera indica* revealed no apparent penetration of the leaf by any part or organ of the epiphyll.

6. The rhizoids of epiphyllous hepatics are especially adapted for the epiphyllous habit by becoming thickened, by flattening out and by being pressed into the cuticle of the leaf, thus firmly attaching the epiphyll to the leaf and preventing its being blown or washed off easily.

7. It is conceivable that the shade produced by the epiphyll, the accumulation of the organic material, the possible excretion of acids and other substances by its rhizoids may have some physiological effect on the supporting leaf.

8. A careful study of the epiphyllous mode of life will, it is believed, bring out some close relations between parasitism and

the epiphyllous habit. Parasitism is possibly an advanced, specialized phase of epiphytism.

The writer is indebted to the Botanical Department of the Johns Hopkins University for the opportunity of going to Jamaica. The writer wishes to thank particularly Professor Duncan S. Johnson for suggesting this problem, for taking the photographs reproduced on PLATE 5, and for helpful advice in carrying on the work. Acknowledgments are due Professor Alexander W. Evans for the determination of most of the epiphyllous hepatics; to Mrs. N. L. Britton of the New York Botanical Garden for the determination of some of the epiphyllous mosses; and to Professors C. C. Plitt and Lincoln W. Riddle for the determination of certain epiphyllous lichens.

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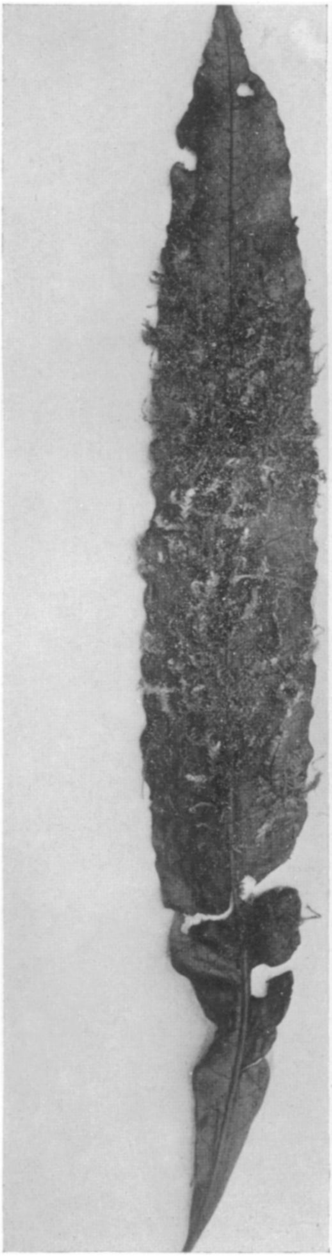
Explanation of plate 1

FIG. 1. Leaf of *Polypodium Phyllitidis*, showing epiphyllous hepatics and mosses.

FIG. 2. Leaf of *Elaphoglossum latifolium*, showing a luxuriant growth of epiphyllous plants; a small wild pine, *Caraguta Sintenesii*, can be seen on the right hand margin.



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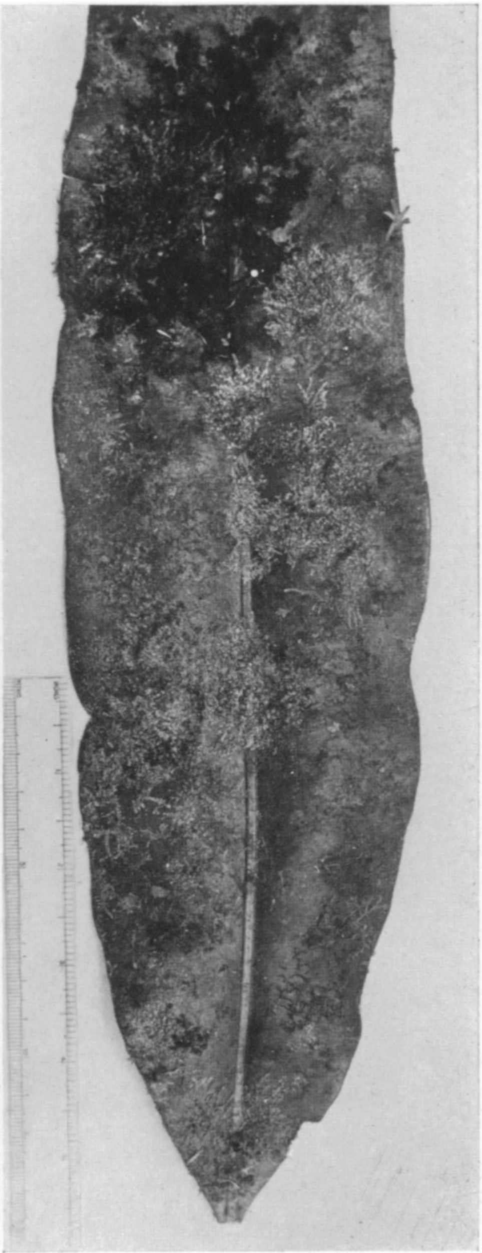

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PESSIN : EPIPHYLLOUS PLANTS OF JAMAICA